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Selective Attention to Semantic and Syntactic Features Modulates Sentence Processing Networks in Anterior Temporal Cortex

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Numerous studies have identified an anterior temporal lobe (ATL) region that responds preferentially to sentence-level stimuli. It is unclear, however, whether this activity reflects a response to syntactic computations or some form of semantic integration. This distinction is difficult to investigate with the stimulus manipulations and anomaly detection paradigms traditionally implemented. The present functional magnetic resonance imaging study addresses this question via a selective attention paradigm. Subjects monitored for occasional semantic anomalies or occasional syntactic errors, thus directing their attention to semantic integration, or syntactic properties of the sentences. The hemodynamic response in the sentence-selective ATL region (defined with a localizer scan) was examined during anomaly/error-free sentences only, to avoid confounds due to error detection. The majority of the sentence-specific region of interest was equally modulated by attention to syntactic or compositional semantic features, whereas a smaller subregion was only modulated by the semantic task. We suggest that the sentence-specific ATL region is sensitive to both syntactic and integrative semantic functions during sentence processing, with a smaller portion of this area preferentially involved in the later. This study also suggests that selective attention paradigms may be effective tools to investigate the functional diversity of networks involved in sentence processing.

Keywords: ATL, fMRI, language, semantics, speech, syntax

Introduction

Identification of neural circuits supporting sentence-level processing in comprehension remains an important but elusive goal in cognitive neuroscience. In order to process a spoken sentence, the listener must not only process word-level phonological, semantic, and syntactic information, but also sentence-level syntactic and semantic properties. Broca's area traditionally has been the central focus in investigating these sentence-level processes (Caramazza and Zurif 1976; Linebarger et al. 1983; Caplan et al. 2000), but more recent work has suggested that Broca's area plays only a limited role in receptive syntax (Grodzinsky 2000). Thus, investigations of syntactic processing have begun to target other cortical regions, particularly the anterior temporal lobe (ATL) (Mazoyer et al. 1993; Dronkers et al. 1994, 2004; Stowe et al. 1999; Friederici and Von Cramon 2000; Friederici et al. 2000; Humphries et al. 2001, 2005; Meyer et al. 2003). Some of these studies are reviewed below to summarize the known response properties of the ATL during sentence comprehension. (In the context of studies of sentence processing, the relevant regions of the ATL are on the lateral aspect and may include [in various studies] structures ranging from those in the superior temporal sulcus to the inferior temporal gyrus.)

Neuropsychological data have provided evidence implicating the ATL in sentence processing. Dronkers et al. (2004) tested patients with focal brain lesions using a sentence comprehension battery that included various degrees of morphosyntactic complexity. Performance on this comprehension test was examined in relation to lesion location. Damage to the left ATL (anterior Brodmann Area (BA) 22) was correlated with deficits in sentence comprehension and appeared to affect comprehension of all but the simplest sentence structures, such as declarative sentences. The authors concluded that the ATL is likely involved in "very basic aspects of morphosyntactic comprehension" (Dronkers et al. 2004).

In functional imaging research, Mazoyer et al. (1993) were among the first to observe that anterior temporal regions respond fairly selectively to sentence-level stimuli. Their positron emission tomography study compared brain activation associated with listening to sentences in the subjects' native language, sentences in an unfamiliar language, pseudoword sentences (content words replaced with nonwords), semantically anomalous sentences, and word lists. Thus, 3 of the stimulus conditions contained syntactic information that was accessible to the subject (the normal sentences, the pseudoword sentences, and the semantically anomalous sentences), whereas the other 2 conditions did not. Mazoyer et al. found that the ATL, bilaterally, was activated during the perception of the 3 syntactically structured stimulus conditions, but not during the perception of the nonstructured stimuli. Broca's area did not show the same response pattern, but rather was activated during the presentation of both word lists and sentences in the subjects' native language, but not during the other structured conditions. Other studies have confirmed that the response to speech stimuli in Broca's area does not track with the presence or absence of syntactic information (Humphries et al. 2001, 2005, 2006).

A number of recent functional imaging studies have corroborated Mazoyer et al.'s findings. Regions of the ATL are more active while listening to sentences than to word lists, scrambled sentences, and environmental sound sequences; pseudoword sentences also appear to drive anterior temporal activation compared with numerous control conditions (Mazoyer et al. 1993; Stowe et al. 1999; Friederici and Von Cramon 2000; Friederici et al. 2000; Humphries et al. 2001, 2005). Again, Broca's area is not consistently activated in sentence minus nonsentence contrasts in these studies.

The above studies all used stimulus manipulations in the context of cognitive subtraction approaches to isolate syntactic processing. Other paradigms have also found evidence that the ATL participates in syntactic aspects of sentence processing. For example, Friederici and colleagues have used anomaly detection paradigms within both electrophysiological and functional magnetic resonance imaging (fMRI) contexts to investigate the functional neuroanatomy of syntactic processing (Rosler et al. 1993; Meyer et al. 2000; Hahne and Friederici 2002; Friederici et al. 2003; among others). Friederici et al.'s event-related potential work suggests that syntactic anomalies elicit an early left anterior negativity, which is suggested to be linked to inferior frontal gyrus and anterior superior temporal function (Friederici and Kotz 2003). Anomaly paradigms using fMRI also have demonstrated increases in left ATL activity due to syntactic violations (Meyer et al. 2000; Friederici et al. 2003).

Although many authors have attributed ATL sentence selectivity to the region's role in syntactic processes, other investigators have considered a possible role for the ATL in combinatorial semantics (Vandenberghe et al. 2002), that is, the process of combining syntactic and lexical-semantic information to derive sentence meaning (e.g., the operations that lead to different interpretations of *Dog bites man* vs. *Man bites dog*). For example, Vandenberghe et al. examined activations associated with reading semantically coherent sentences, semantically random sentences (content words randomly chosen), and scrambled versions of each of these stimuli. Consistent with the studies discussed above, Vandenberghe et al. identified a region of the ATL that responded preferentially to structured sentences independently of the semantic coherence of the stimuli. However, they also found a subarea of the ATL that showed greater activity for structured sentences than for scrambled sentences, but only when the structured sentences were semantically coherent. The authors argued that this interaction between syntax and semantics indicates that this ATL area might be involved in compositional semantics. Humphries et al. (2006) conducted a similar experiment in which stimuli were sentences, semantically random sentences, pseudoword sentences, or scrambled versions of each. Although they replicated the main effect of syntactic structure in the ATL (activation greater for sentences than unstructured noun lists), they found that the semantic manipulations produced effects in the opposite direction in a subregion of the ATL with normal (semantically congruent) sentences leading to greater activation than semantically random or pseudoword sentences. Task differences (one-back vs. ratings of meaningfulness) were cited as a possible explanation for the discrepancy. Nonetheless, both studies did uncover evidence for a possible partitioning of the ATL into one region that is primarily responsive to syntactic structure and another that is sensitive to compositional semantic processes.

Both Vandenberghe et al. and Humphries et al. used stimulus manipulations to assess the relative contributions of syntactic versus combinatorial semantic computations in the ATL during sentence processing. One problem with this approach is that it involves the processing of atypical sentences (semantically random and/or scrambled sentences), and it is unclear how this relates to processing normally structured and semantically coherent structures because it is difficult or impossible to manipulate one of these dimensions without affecting the other. A similar problem plagues studies that examine brain responses to syntactic violations: it is unclear whether this manipulation highlights regions involved in normal syntactic computation, or regions that are reactive to error detection (or both).

The goal of the present study was to assess the relative contributions of the ATL to syntactic versus combinatorial semantic operations using a paradigm that does not rely on processing atypical sentences, or on stimulus manipulations at all. To this end, we employed a selective attention paradigm to modulate attention between syntactic and sentence-level semantic processes. Selective attention has been shown to effectively modulate neural activity in visual, auditory, and linguistic tasks (Corbetta et al. 1990; Platel et al. 1997; Chawla et al. 1999; Ni et al. 2000; Von Kriegstein et al. 2003; Cant and Goodale 2007). In an fMRI study, we asked participants to attend either to syntactic or compositional semantic aspects of normally structured and semantically coherent sentences. Vigilance was monitored by including occasional syntactic or semantically anomalous sentences, which crucially, were excluded from the fMRI analysis. This paradigm has the advantage that stimuli can remain constant across conditions (sentences were in fact *identical* in both the semantic and syntactic attention conditions across subjects) and we can examine brain responses during the processing of normally structured and semantically coherent sentences. We were particularly interested in determining whether 2 distinct ATL regions would be identified using this paradigm: one that is primarily sensitive to syntactic operations and therefore should show increased activation during attention to syntactic properties of sentences, and another region primarily sensitive to compositional semantic operations and therefore should show increased activation during attention to compositional semantic properties of sentences.

Regions of interest (ROIs) in the ATL were localized by identifying areas more active for correct sentences than noun lists. We then determined whether attention to syntactic or combinatorial semantic features could modulate activity in these ATL regions. If the ROIs are involved in syntactic computations, it is predicted that attending to the syntactic information of correct meaningful sentences would lead to an increase in the blood oxygenation level–dependent (BOLD) response in these regions. Alternatively, if ATL regions are recruited in combinatorial processing, attending to the overall meaning of correct meaningful sentences should modulate neural activity.

Materials and Methods

Participants

Fourteen right-handed native English speakers (9 males, 5 females; mean age = 23 years, range 19–31) participated in this study. All participants were free of neurological disease (self report) and gave informed consent under a protocol approved by the Institutional Review Board of the University of California, Irvine.

Experiment Design and Stimuli

Our event-related experiment consisted of the subject listening to individual sentences and, in separate runs, either making syntactic acceptability or semantic anomaly judgments. Specifically, in the syntactic task, subjects were instructed to press a response button when they heard a syntactic error, whereas in the semantic task they were instructed to press a response button when they heard a semantic anomaly. Subjects were given several examples of each error type and completed practice trials prior to scanning to ensure mastery of both tasks.

Unacceptable/anomalous sentences occurred in 20% of trials (10% syntactically unacceptable, 10% semantically anomalous), and occurred at the same frequency in both task conditions so that the only variable manipulated was the task (pressing a button upon detecting a syntactic error or detecting a semantic anomaly). A given sentence only contained one type of violation. Only the correct (error-free) sentences were used in the analysis to avoid measuring activations associated with error detection.

Subjects participated in 5 scanning runs. The first was a "localizer" designed to identify regions that demonstrate relatively selective responses to sentences, as have been found in several previous studies. This run consisted of 20 sentences and 20 noun lists presented in a random order, again following prior experiments (Mazoyer et al. 1993; Humphries et al. 2006). In this localizer run, subjects were asked to listen attentively to all stimuli, but made no overt responses (i.e., "passive listening").

In 2 of the remaining runs, subjects were instructed to press a button whenever they heard a syntactic violation. In the 2 other runs, subjects were instructed to press a button when a semantic anomaly occurs. Button box responses to the error/anomaly detection tasks were recorded. These responses were used to ensure that the subjects were attending to the correct sentence features and to remove false alarm trials from the imaging analysis. Across subjects, the order of the syntactic and semantic runs was counterbalanced. Each run consisted of 60 trials (48 correct, 6 syntactically unacceptable, 6 semantically anomalous). Each trial consisted of a warning tone (1 s), the sentence (3 s), and a rest period of 10, 12, or 14 s.

All stimuli were recorded by a male speaker and edited using Audacity sound-editing software. Stimuli in the localizer run were sentences and noun lists, matched for length (see Appendix A). The sentences included active and passive constructions, each containing either a prepositional phrase or relative clause. The noun lists consisted of common nouns, each one to 3 syllables in length. The nouns were recorded as individual words, rather than as a list with "list intonation." The nouns were arranged into lists pseudorandomly with the constraint that the lists matched the sentences in terms of overall syllable length. We used noun lists (versus including verbs and closed-class items) in order to decrease the probability that subjects would unconsciously try to extract sentence-like structure from the lists.

Stimuli in the experimental runs (see Appendix A) were sentences of the form (noun phrase–aux verb–noun phrase), where one of the noun phrases was modified by a prepositional phrase, for example:

The vase *on the desk* was holding some flowers.
The mechanic was fixing a bus *in the garage*.

Syntactic violations were restricted to number agreement between determiner and noun (*A vases, or *those vase) or between noun and verb (*the vases was...). This allowed us to position the violation in early, middle, or late stages of the sentence, thus requiring subjects to attend to the entire sentence. The prepositional phrase allowed us to ensure that subjects were processing the structure hierarchically rather than simply using an adjacency strategy (*the vases on the desk was...).

Semantic (i.e., pragmatic) violations involved thematic role incompatibility (#the flowers were holding the vase...), or incompatibility between the noun and the prepositional phrase (#the desk on the vase...). Again, this allowed us to place the anomaly in an early, middle, or late position in the sentence. A given error sentence contained only one type of violation. No subject heard more than one version of a given sentence, but sentences were balanced equally across subjects, and task conditions; i.e., the exact same sentences appeared in both task conditions, thus ensuring that nuisance variables such as word frequency, concept familiarity, and length were precisely controlled.

fMRI Data Acquisition and Processing

Data were collected at the University of California Irvine's Phillips-Picker 1.5 Tesla scanner. A high-resolution anatomical image was acquired, in the axial plane, with a 3D fat-suppressed gradient recalled echo pulse sequence for each subject (field of view [FOV] = 250 mm, time repetition [TR] =13 ms, flip angle = 20°, voxel size = 1 mm × 1 mm × 1 mm). Functional MRI data was collected using single-shot echo-planar imaging (FOV = 250 mm, TR = 2 s, TE = 40 ms, flip angle = 90°, voxel size = 1.95 mm × 1.95 mm × 5 mm). MRIcro (Rorden and Brett 2000) was used to reconstruct the high-resolution structural image, and an in-house Matlab program was used to reconstruct the echo-planar images. Functional volumes were aligned to the sixth volume in the series using a 6-parameter rigid-body model to correct for subject motion (Cox and Jesmanowicz 1999). Each volume then was spatially filtered (full width half maximum = 8 mm) to better accommodate group analysis.

Data Analysis

Analysis of Functional NeuroImaging software (http://afni.nimh.nih.gov/afni) was used to perform a multiple regression analysis on the time course of each voxel's BOLD response for each subject (Cox and Hyde 1997). Regressors for each condition (passive listening to sentences, passive listening to noun lists, perception of correct sentences during the syntactic task, perception of correct sentences during the sentence-level semantic task, and perception of incorrect/anomalous sentences during both tasks) were generated. These regressors (in addition to motion correction parameters and the grand mean) were convolved with a hemodynamic response function to create predictor variables for analysis. An F-statistic was calculated for each voxel, and activation maps were created for each subject to identify regions that were more active while listening to each type of stimuli compared with baseline scanner noise. The functional maps for each subject were transformed into standardized space and resampled into 1 × 1 × 1 mm voxels (Talairach and Tournoux 1988) to facilitate group analysis.

As reviewed in the introduction, previous studies have found 1) that a region in the ATL is relatively sentence-specific in its BOLD response and 2) this region contains 2 subareas: one which appears to be more responsive to syntactic processing and another which appears to be more responsive to compositional semantic processing. As a part of our analysis strategy, therefore, we sought to identify an ATL ROI that is relatively sentence specific, and then to determine if subregions were modulated by the syntactic versus compositional semantic task. We defined the ATL ROI as previous studies have, by contrasting sentences with noun lists: a repeated-measures t-test was performed to identify voxels that were more active during passive listening to sentences than to noun lists across subjects.

Analysis of Attention Modulation

Analysis of attentional effects proceeded along 2 paths. In one analysis, we mapped regions that were responsive to the perception of sentences during the syntactic task versus rest, the semantic task versus rest, or the conjunction of the 2. The resulting activation maps then were examined in relation to the localizer-defined ROI. In a second analysis, we assessed whether there were any differential task effects within the ATL localizer-defined ROI by directly contrasting the 2 attentional task conditions.

Additionally, although inferior frontal regions were not identified by the sentence localizer, we explored the effects of our task manipulation on inferior frontal regions due to their frequent implication in sentence processing via various anomaly paradigms and stimulus manipulations. ROIs were defined by identifying inferior frontal regions whose activation passed threshold during the perception of correct sentences in either the syntactic or semantic task, or in both tasks. The response properties of these ROIs were further described by calculating across subjects the mean peak BOLD response during each task as well as for during the passive listening to sentences and noun lists.

Results

Behavioral Data

Response accuracy rates approached ceiling performance in both the syntactic (M = 95.7%) and semantic (M = 98%) tasks. A repeated-measures t-test indicates that there was no significant difference between performance on the 2 tasks: $t(13) = 0.61$, $P = 0.55$.

Sentence Localizer

A voxel-wise repeated-measures t-test identified anterior temporal regions that were more active during passive listening to sentences compared with noun lists across subjects. Voxels responding more to sentences than noun lists ($P = 0.01$) were found in the left ATL (–47 17 –18) and right ATL (52 18 –20) (see Fig. 1*A*). No other regions were more active for sentences than for noun lists at this threshold. The relatively liberal threshold of $P = 0.01$ was used because 1) the "localizer" scan was comprised of a single run, and thus did not contain as many stimuli as has been typically used in previous studies of sentences compared with unstructured word strings and 2) this activation focus was used as an independently identified ROI for subsequent analyses; therefore we did not want a stringent threshold to exclude regions from this ROI that may be sensitive to sentence structure.

Overall Task Effects

Bilateral temporal and frontal regions typically implicated in speech processing were active during the perception of correct sentences in one or another task condition (or both) compared with rest (see Fig. 1*B*). (Correct sentences were defined as sentences that did *not* contain a syntactic or semantic error and were identified as correct by the subject. Only responses to correct sentences thus defined were analyzed; all results reported below are from this set of correct items.) The $P = 0.005$ threshold (0.001 is typical) was used to map the task effects to ensure that close, but subthreshold effects were not obscured in this descriptive analysis. Regions that passed threshold during both task conditions included a large swath of activation along the superior and middle temporal gyri, as well as some smaller clusters in posterior frontal cortex. Regions that were significantly active during the semantic but not the syntactic task included a large left posterior temporal area (#2 in Fig. 2*A*), sites in the ATL bilaterally, and smaller clusters in posterior frontal cortex. Focal activations that reached threshold for the syntactic, but not the semantic task were also found in posterior temporal areas, dorsal STG, ATL, and several frontal regions including premotor areas and Broca's region. Table 1 lists activation foci in Talairach coordinates, and Figure 2 shows amplitudes for both tasks in each activation focus (relative to rest), as well as the amplitudes for sentences and noun lists in the sentence localizer scan. Note that the relatively small differences in amplitude between task conditions is not surprising given that in both conditions, subjects are processing both syntactic and compositional semantic information. Our methodological goal was to use a selective attention manipulation to modulate the baseline activity in order to highlight relative processing differences between regions. It is clear from the data presented in Figures 1 and 2, that the study was successful in this respect.

Our theoretical goal in this study was to examine task effects in ATL regions. The whole brain activation maps show that ATL regions, generally, appear to contain functionally differentiated

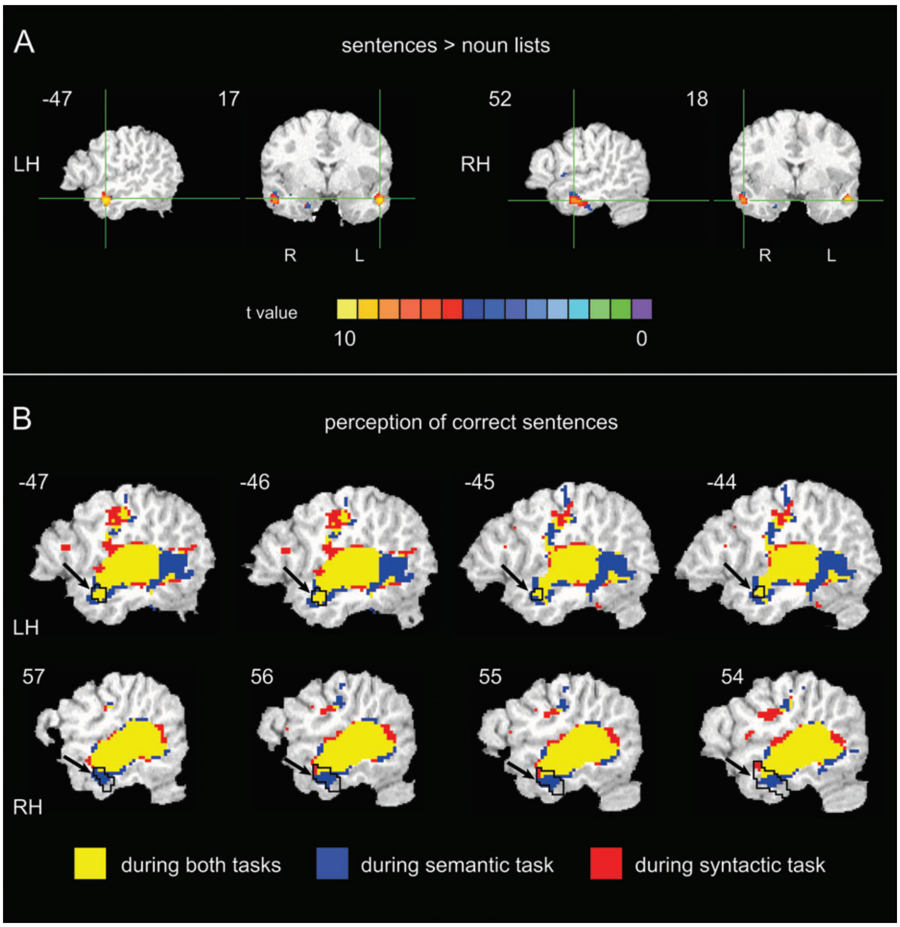

Figure 1. (*A*) Anterior temporal regions more active for sentences than noun lists in the localizer run across subjects ($P < 0.01$). (*B*) Regions active during the perception of correct sentences in both tasks, and each task respectively, compared with rest across subjects, ($P < 0.005$). Regions indicated by an arrow and outlined in black correspond to regions identified by the sentences > noun list contrast shown in (*A*).

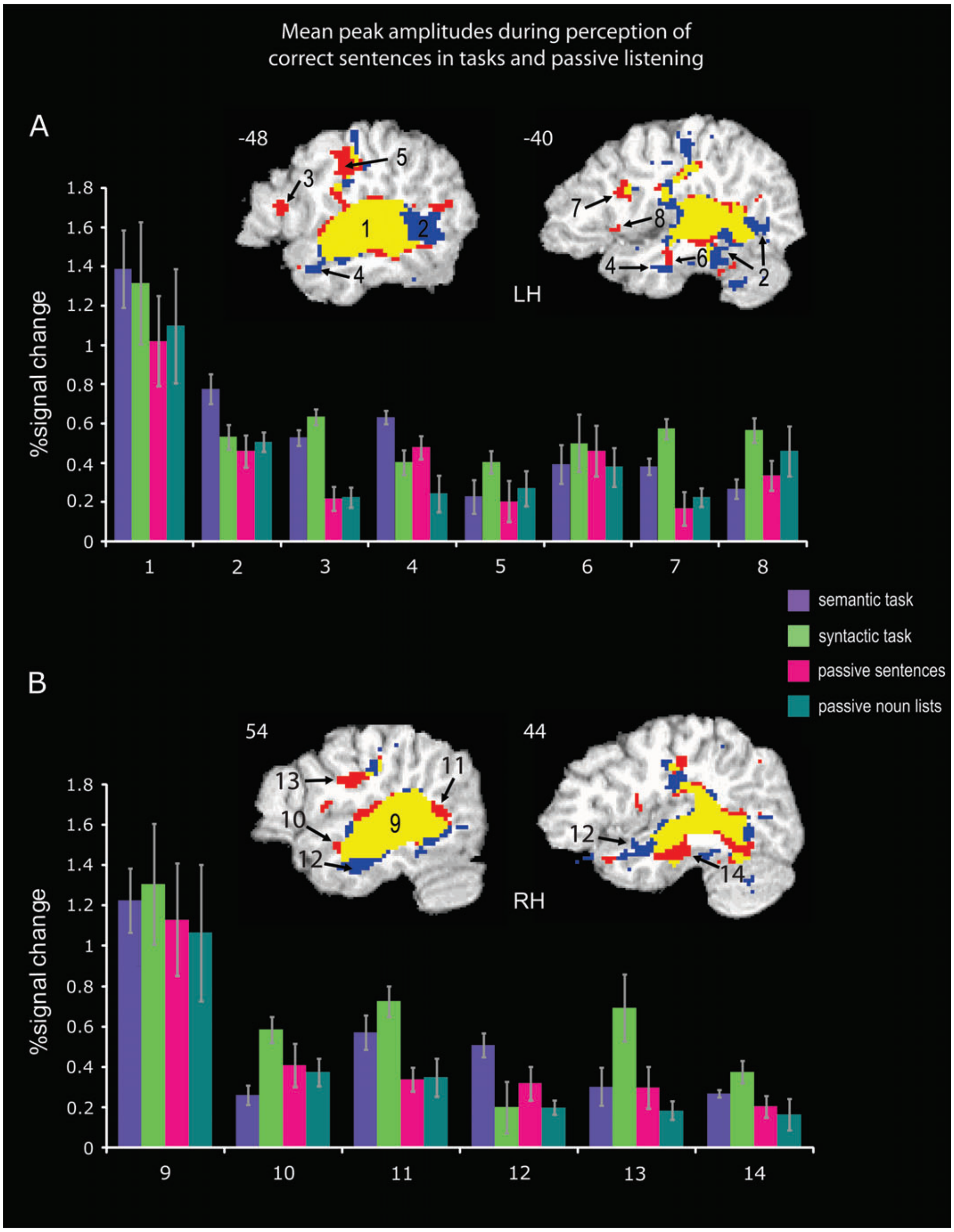

Figure 2. Mean peak amplitudes of selected clusters in the left (*A*) and right (*B*) hemispheres active during the perception of correct sentences in at least one task, compared with rest ($P < 0.005$), averaged across trials and subjects. Mean peak amplitudes are shown for each task, as well as for the passive listening to sentences and noun lists in the localizer run. Each cluster's number corresponds to the activation map, as well as to Table 1. Error bars represent 95% confidence intervals.

subfields, some of which are significantly activated only for the semantic task, some only for the syntactic task, and some for both tasks. But, activations associated with sentence processing compared with a resting baseline could be attributable to any number of processing stages ranging from acoustic analysis to compositional semantic computations. For this reason, we were particularly interested in the relation between the task effects on the one hand, and the sentence localizer ROIs on the other, as the sentence localizer should isolate sentence-level processes. Within these ROIs (black outlines in Fig. 1*B*), activation patterns were not uniform. Some clusters were active for the semantic task only (bilateral), some smaller clusters were active for the syntactic task only (right hemisphere), and some were active for both tasks (bilateral). The bulk of the left hemisphere sentence ROI responded to both tasks, whereas the right hemisphere ROI appeared more heterogeneous.

Thresholding effects in the above analysis, however, could either 1) obscure important differences in the modulation of the ATL ROI by the 2 task conditions (e.g., if both tasks are above threshold but nonetheless differ significantly from one another), or 2) falsely suggest that differences between task conditions exist, when they do not (e.g., if one task barely

Table 1

Talairach coordinates for the sentence localizer ROIs, as well as for the largest clusters (i.e., contiguous voxels) that are active during the perception of correct sentences in at least one task, compared with rest ($P < 0.005$), averaged across trials and subjects

	Region	Brodmann area(s)	Center of mass				Peak during preferred task		
			x	*y*	*z*	*t*	*x*	*y*	*z*
Sentence localizer	L STG	38	−47	17	−18				
	R STG	38	52	18	−20				
Active for both tasks	L temporal lobe (1)	21, 22, 38, 41, 42	−46	−7	−1				
	L precentral gyrus	6	−47	1	32				
	L IFG/MFG	46	−38	29	17				
	R temporal lobe (9)	21, 22, 38, 41, 42	49	−8	2				
	R premotor	6, 9	49	3	28				
Semantic task preference	L STG (4)	38	−44	17	−23	5.67	−51	12	−10
	L MTG (2)	21, 22, 37	−47	−31	0	5.56	−47	−19	−5
	L precentral gyrus	6	−40	−3	40	4.2	−41	−3	40
	L MFG	10	−31	35	16	5.16	−29	27	22
	R STG (12)	21, 38	56	10	−20	6.25	57	9	−20
	R MFG	9	46	3	21	5.75	46	1	21
Syntactic task preference	L STG/MTG (6)	21, 38	−39	6	−19	4.13	−39	5	−23
	L IFG/MFG (5)	9, 44, 45	−48	7	30	5.92	−49	3	29
	L IFG (3)	45, 46	−48	38	9	4.23	−47	37	11
	R STG/MTG (10)	21, 22, 38	61	9	−13	4.85	61	11	−9
	L IFG/MFG (7)	44, 45, 46	−38	33	14	4.67	−38	31	17
	L IFG (8)	47	−36	32	−5	4.14	−41	35	−5
	R STG (14)	38	41	2	−14	4.72	48	8	−15
	R STG (11)	22	51	−31	6	5.4	43	−33	3
	R precentral gyrus	6	47	−1	36	3.99	47	−5	38
	R IFG (13)	9, 44, 45	54	11	23	4.24	54	11	23

Note: For clusters demonstrating a task preference, the *t* value and Talairach coordinates of the cluster's peak voxel are listed. The numbers in parentheses correspond to the numbers in the activation maps and mean peak amplitude graphs in Figure 2.

Abbreviations: STG = superior temporal gyrus, IFG = inferior frontal gyrus, MFG = middle frontal gyrus, MTG = middle temporal gyrus.

reaches threshold for activation and the other just misses threshold). For this reason, we carried out a direct contrast between the 2 task conditions to see if any voxels within the sentence localizer ROI were indeed differentially affected by the 2 tasks. This analysis resulted in the following observations. First, most of the sentence localizer ROI responded equally to the 2 task conditions. In fact, at a *P*-value threshold of 0.01, there were no voxels in either the left or right ROI that were significantly active in one task condition compared with the other. Second, at a slightly relaxed threshold of 0.025, however, a cluster of voxels in the left ROI was found to be more active during the semantic task compared with the syntactic task (BA 38, −48, 20, −15; Fig. 3). And third, there were no voxels within either the left or right ROIs that were significantly greater for the syntax over the semantic attention task even at very liberal thresholds ($P = 0.10$). Thus, within the sentence localizer ROI, task-specific selective attention effects were only found for the compositional semantic attention task, only in a relatively small fraction of the ROI voxels, and only in the left hemisphere. Within the larger fraction of the ROI that did not respond differently to the 2 task conditions, we noted that activation levels in left hemisphere were nonetheless greater for both of the attention conditions than for the passive listening condition from the sentence localizer (Fig. 3); there was no difference between the task conditions and the passive listening conditions in the right hemisphere ROI ($P > 0.1$). In sum, 1) the *left* hemisphere sentence localizer-defined ROI contained 2 subregions: a relatively large subregion that was equally modulated by *both* selective attention tasks (tasks > passive), and a smaller subregion that was only modulated by the compositional semantic attention task (semantic task > syntactic task = passive listening); 2) the *right* hemisphere sentence localizer-defined ROI was not modulated by either attention task (tasks = passive).

Sentence Processing in the Frontal Lobe

The focus of our investigation was on the response properties of the ATL. However, we briefly address here frontal lobe activity during the tasks and sentence localizer for comparison and descriptive purposes. Coinciding with Mazoyer et al. and Humphries et al.'s findings, our sentence localizer did not identify any frontal regions more active during passive listening to sentences compared with noun lists. Therefore, frontal ROIs were selected for investigation based on other criteria, namely their location in the left inferior frontal lobe and their activation at $P < 0.005$ during the perception of correct sentences in one or both tasks. Portions of BA 46 (−48 38 9) and the frontal operculum (−36 32 −5), as well as a region partially including BA 44 (−38 33 14) were active during the perception of correct sentences during the syntactic task, but did not pass threshold for the semantic task. Adjacent to the BA 46 region responding preferentially to the syntactic task, we also identified a subregion whose activation only passed threshold during the semantic task, (−31 35 16), as well as a region highly active during both tasks (−38 29 17). Comparison of mean peak amplitudes of these task-driven regions for each subject during the sentence localizer reveals that the syntax task-preferring BA44 region is more active during the lists than the sentences. The other frontal ROIs are equally active during listening to the sentences and lists in the localizer (see Fig. 2).

Discussion

The present study investigated the response properties of the ATL during the perception of normal, error-free sentences. BOLD responses were first recorded during passive listening to sentences and noun lists to define an ROI with relatively selective responses to sentence-level stimuli, as had been observed in several previous studies. Then, syntactic and

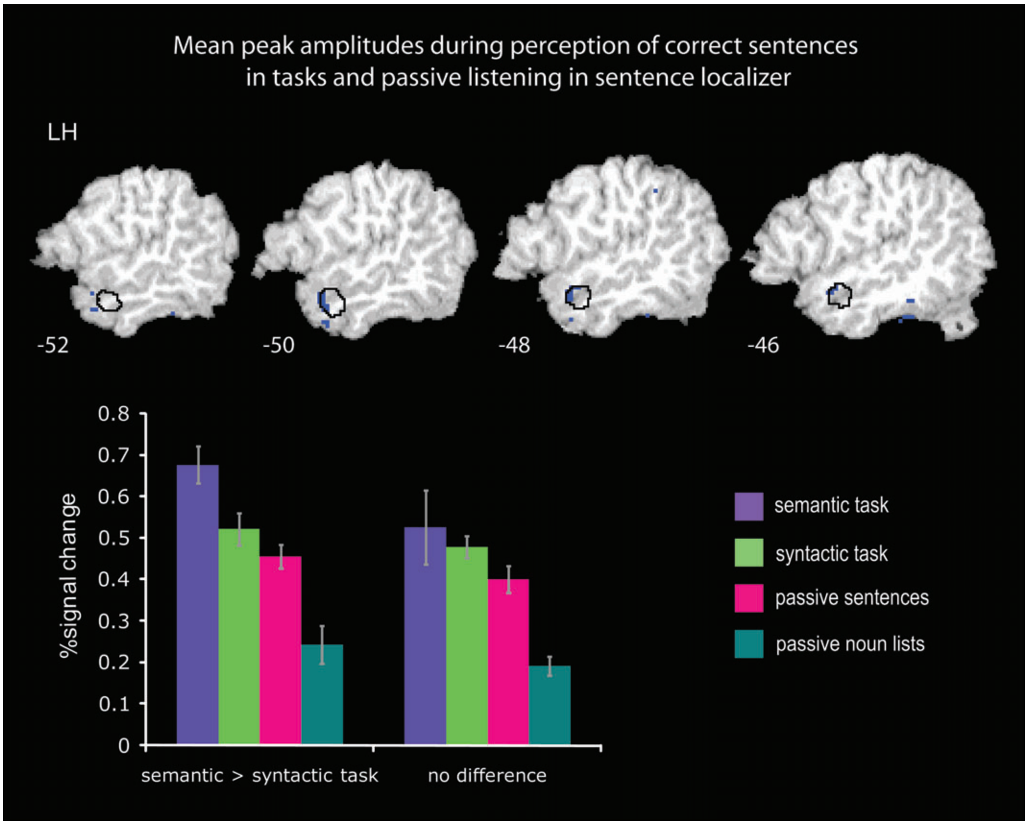

Figure 3. ATL subregions more active during the perception of correct sentences during the semantic task than the syntactic task as determined by a voxel-wise paired samples *t*-test ($P < 0.025$). Regions outlined in black correspond to regions identified by the sentences > noun list contrast shown in Figure 1*A*. The accompanying bar graphs represent mean peak amplitudes for the portion of the sentence localizer ROI that is identified as having a semantic task preference via the *t*-test mentioned above (in blue) and for the portion not demonstrating this preference, respectively. Error bars represent 95% confidence intervals.

compositional semantic error detection tasks were employed to modulate attention to syntactic or compositional semantic properties. Consistent with previous research, we identified a large perisylvian network that responded to listening to sentences compared with rest (Mazoyer et al. 1993; Dronkers et al. 1994, 2004; Friederici and Von Cramon 2000; Friederici et al. 2000; Humphries et al. 2001, 2005), and a much more focal site in the ATL bilaterally that responded more during listening to sentences compared with listening to lists of words (Humphries et al. 2001, 2005; Vandenberghe et al. 2002). In addition, the left ATL region that we identified as having a semantic task preference (#4 in Table 1 and Fig. 2), significantly overlaps with the left ATL subregion that Vandenberghe et al. found to have greater activity for structured sentences than for scrambled sentences, but only when the structured sentences were semantically coherent. (This conclusion is based on the Talairach coordinates and the number of voxels in the cluster reported by Vandenberghe et al. Both regions are in BA 38.)

Although whole brain analyses of task effects suggested task-dependent subregions of this ATL ROI, direct contrasts between the syntactic and semantic tasks within the ROI showed 1) that most of the voxels in both the left and right hemisphere ROIs responded equivalently to the 2 task conditions, and 2) that a *subset* of voxels in the left ROI were more active during the compositional semantic task than the syntactic task. The lack of a syntactic effect in the ATL ROI cannot be attributed to general task difficulty differences as performance did not differ on the 2 tasks, nor can the lack of an effect result from a general failure of the syntactic task to elicit *any* kind of modulatory response in the brain, as several regions outside the ATL ROI were modulated by the syntactic task relative to the semantic task (e.g., see left frontal regions #5, 7, and 8 in Fig. 2), and within the left ATL ROI, the syntactic task lead to greater activation than the passive listening task in the sentence localizer scan. In sum, the sentence-selective ATL ROI appears to be equally sensitive (or insensitive) to syntactic and compositional semantic tasks, except for a small subregion in the left ROI, which is differentially modulated by attention to compositional semantic features of the stimuli relative to a task that requires sensitivity to syntactic features. Below, we interpret these findings within the context of previous sentence processing neuroimaging and neuropsychological research, as well as discuss the benefits of implementing a selective attention paradigm to investigate the neural correlates of sentence processing.

Response Properties of Anterior Temporal Cortex

Previous research has implicated the anterior temporal cortex in processing speech containing syntactic structure (Mazoyer et al. 1993; Humphries et al. 2001, 2005; Vandenberge et al. 2002; Meyer et al. 2003). Similarly, in the present study, we found that bilateral ATL regions demonstrated an increased BOLD response while listening to sentences compared with noun lists. A major question is whether this ATL activation reflects semantic integration operations, some form of syntactic computations, or both. These alternatives are difficult to distinguish in previous studies because manipulations of one aspect of a linguistic string (its syntactic or semantic properties) necessarily affects processing within the other, and because the effects of processing syntactically or semantically altered strings is unclear. Our selective attention task attempts to avoid these problems by inducing attention to, and therefore enhancing activation of, processes involved in one of these 2 properties of normal sentences.

One subregion of the sentence-defined left hemisphere ATL ROI responded more during attention to compositional semantic properties than during attention to syntactic properties of the same (error-free) sentences. This finding suggests that at least a portion of this ROI is more involved in semantic than syntactic operations. However, the subregion that showed this effect represented only a small fraction of the entire sentence-defined ATL ROI. The majority of the ROI did not differentially respond to the 2 task conditions. This nondifferential response could have occurred because the region is sensitive to neither attentional task, or because it is sensitive to both attentional tasks equally. A comparison of the activation levels for the 2 attention tasks relative to the passive listening task in the sentence localizer scan suggests the latter possibility for the left hemisphere ROI. That is, both the semantic and syntactic attention tasks lead to greater activation in the nondifferential response subregion of the sentence-defined ROI than did the passive listening condition in the localizer. This increase in activation levels during the attention tasks might have resulted from either better signal to noise in the attention runs where we collected more trials, or from a generalized attention effect, not specific to language processing. However, this seems unlikely given that the right hemisphere ROI did not show the same effect, nor did several other regions throughout the brain (e.g., regions #2, #4, #6, and #13, do not show generalized task > passive effects). We therefore tentatively conclude that most of the left hemisphere sentence-defined ROI is modulated by both attention to compositional semantic and syntactic features of sentences, whereas a smaller portion is only modulated by attention to compositional semantic features. This, in turn, may indicate that this region as a whole participates in both syntactic and compositional semantic operations. It will be instructive in future studies to test the specificity of these selective attention effects (i.e., are they specific to sentence-level attention tasks?), and whether attention to different syntactic properties of sentences might yield different results.

Although portions of the ATL show relatively selective responses to syntactically structured sentence-level stimuli, and although this region appears to increase its response during attention to syntactic properties of sentences, it is nonetheless unlikely that the ATL alone supports syntactic computations in sentence processing. For example, lesion evidence indicates that ATL damage can disrupt sentence comprehension, but only for relatively more complex items such as morpho-syntactically complex sentences (Dronkers et al. 2004) and ambiguous sentences (Zaidel et al. 1995). Further, even substantial bilateral ATL atrophy in semantic dementia does not produce the kinds of syntactic deficits one would expect if the ATL was a central hub for syntactic computations (Garrard and Hodges 2000). Semantic dementia patients, however, do present with significant domain-general conceptual-semantic deficits (i.e., the deficit is not restricted to the linguistic domain). Perhaps the ATL is broadly involved in conceptual-semantic integration or access (Patterson et al. 2007), with a portion of it dedicated to interacting with linguistically constrained semantic integration. Clearly, a great deal of work is needed to sort out ATL involvement in this range of processes. It will be important in this effort to clearly distinguish between domain-general conceptual-semantic processes versus language-related lexical and combinatorial semantic processes.

Semantic Processing in the Posterior Temporal Lobe

The severity of semantic deficits in semantic dementia has led several groups to emphasize the role of the anterior temporal regions in word-level semantic processes (Scott et al. 2000; Gorno-Tempini et al. 2004; Spitsyna et al. 2006) (although, again it is important to distinguish lexical from conceptual-semantic processes). More traditional accounts of lexical-semantic processing based on focal lesion data (typically stroke) (Hart and Gordon 1990) as well as functional imaging studies (Binder et al. 1995) have emphasized the posterior temporal lobe (Hickok and Poeppel 2000, 2004, 2007). The present study found a relatively large region of cortex in the left posterior temporal lobe that appeared to be more sensitive to combinatorial semantic than syntactic processes (see Figs 1*B*, 2*A*). This finding is consistent with the view that posterior temporal regions are playing a significant role in some aspect of semantic processing. Other recent functional imaging studies have also emphasized a role for posterior temporal and temporal-parietal areas in semantic processing (Humphries et al. 2006). It is unclear whether these posterior areas are involved in linguistic-specific, or domain-general semantic processes, and it is still unclear what form of semantic processes might be involved.

Role of Frontal Cortex in Sentence Processing

Although the specific aim of the present study was to further characterize the role of the ATL in sentence processing, because Broca's area has figured prominently in hypotheses regarding syntactic processing in the brain (Just and Carpenter 1992; Just et al. 1996; Stromswold et al. 1996; Caplan et al. 1998; Dapretto and Bookheimer 1999; Caplan and Waters 1999; Martin 2003), we also examined response properties of Broca's region. Our results indicate that inferior frontal regions typically identified in the sentence processing literature are modulated by attention to syntactic or sentence-level semantic properties (see Fig. 2). However, none of these inferior frontal regions are more active during passive listening to sentences compared with noun lists (using the threshold at which ATL sentence ROIs were identified). This result coincides with the hypothesis that Broca's area's involvement in speech processing is task dependent, and recruited during high-load conditions (e.g., the participants' increased analysis of and attention to sentence properties that are typically processed automatically) (Just and Carpenter 1992; Love et al. 2006).

Conclusion

Our findings are consistent with the view that a portion of the ATL is involved in sentence-specific processing. A majority of this region, particularly on the left, appears to be sensitive to both syntactic and compositional semantic properties of sentences, with a smaller fraction sensitive primarily to compositional semantic properties. In addition, we have demonstrated that a selective attention paradigm can be an effective tool to investigate the cortical components of natural sentence processing.

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Appendix A

Correct Sentences Presented during Selective Attention Tasks

The goat by the farmhouse was eating some grass.
A chicken near the barn was pecking the ground.
The host of the reception was serving some cookies.
That girl in the park was playing the violin.
The puppies in the yard were chasing a kitten.
That fence near the school was obscuring the playground.
That woman with the hat was buying a dress.
The wool in the sweater was itching the boy.
A swimmer in the pool was splashing the lifeguard.
A baker in the café was kneading the dough.
The rainbows near the creek were distracting the tourists.
Those monsters in the movie were frightening the crowd.
That train at the station was transporting the livestock.
That quilt on the sofa was hiding a stain.
The teenager in the van was honking the horn.
The trap on the wall was catching some mosquitoes.
A crab in the ocean was pinching the surfer.
A janitor at the mall was washing the windows.
Those pots near the stove were cluttering the kitchen.
The guards by the door were protecting the senator.
The members of the union were raising their wages.
The turtles in the pond were biting the ducks.
That archer near the target was aiming the arrow.
A horse on the track was disobeying the jockey.
The pigs in the pen were enjoying the mud.
Some children at the fair were petting the animals.
That guide at the museum was conducting a tour.
The rat in the cellar was clawing the floor.
The cones in the street were redirecting the traffic.
Those hikers on the trail were following the signs.
The vase on the desk was holding some flowers.
The questions on the test were puzzling the student.
The rooster in the coop was guarding the hens.
The rabbit behind the shed was chewing the lettuce.
The king at the banquet was honoring his knights.
The truck on the highway was passing the accident.
Some customers in the store were asking the clerk.
That actor on the set was rehearsing a scene.
The leopard in the jungle was stalking some monkeys.
The artist with the canvas was painting the portrait.
A robber behind the bank was stealing some money.
Those lawyers in the boardroom were signing the contract.
Those geese above the meadow were circling the lake.
That captain of the ship was avoiding an iceberg.
The daughter of the queen was hugging the hero.
The giraffe in the zoo was devouring the leaves.
The bartender at the party was making some drinks.
A clown in the circus was juggling three balls.
A pilot was steering the airplane on the runway.
Those insects were invading the fruit in the basket.
Those bugs were irritating the zebra near the stream.
That craftsman was designing a plaque for the mayor.
The mom was taking the toddler to the crib.
The cowboy was riding this bull in the ring.
A butler was polishing the silver in the chest.
A ghost was haunting that house near the cemetery.
Those farmers were milking these cows in the pasture.
The tractors were plowing the field near the road.
That barber was cleaning the scissors in the jar.
That painter was bringing some brushes from the workshop.
The boss was questioning the interns in the office.
The congressman was kissing the babies in the crowd.
A mouse was snatching the cheese from the platter.
Those firemen were saving a family on the roof.
Those workers were hammering the nails into the wood.
Those cops were tackling the criminal on the sidewalk.
That crook was watching the shopper by the register.
A germ was spreading a virus through the region.
The prince was admiring the maiden at the feast.
The team was winning the game at the stadium.
An owl was tracking a possum in the woods.
Those pirates were raiding the village on the island.
That car was trailing the men on the motorcycles.
The writer was describing the plot of the story.
The tornado was flattening a town on the plain.
The storm was demolishing the hotels near the beach.
The witness was telling the truth in the courtroom.
The drummers were practicing a song in the basement.
The bride was thanking the guests at the reception.
The blanket was covering the sheets on the bed.
Some chemicals were corroding the tools on the rack.
Some ants were swarming the food at the picnic.
A priest was announcing his schedule in the chapel.
The dancers were performing a ballet in the show.
Those plants were producing some pollution in the air.
That wrestler was pinning his rival on the mat.
The bear was defending her cubs in the den.
The lions were pursuing the gazelles in the hills.
The spiders were spinning their webs around the pole.
Those jets were bombing the forts near the border.
The choir was singing a hymn after the sermon.
The mechanic was fixing a bus in the garage.
Those butchers were slicing some meat behind the counter.
The doctor was comforting the patient in the chair.
The housekeeper was changing the linens in the suite.
A sailor was adjusting the sails of the boat.

Syntactic Violations

A clouds in the sky were blocking the sunshine.
Those athlete at the gym was lifting some weights.
A squirrels were gathering the nuts in the forest.
A scientists were observing the cells in the tube.
A *tailor* in the city *were* altering the gown.
Those *accountants* at the firm *was* counting the profits.
The *sharks* around the reef *was* hunting the seals.
The *plumber* with the glasses *were* installing the sink.
The fans in the bleachers were heckling *a opponents*.
The hurricane from the east was destroying *those bridge*.
The coach was encouraging the runners in *those race*.
That fraternity was hosting those meals for *those dorm*.

Semantic Violations

The table at the man was dealing the cards.
Those tanks in the soldiers were shooting the enemy.
That nest in the robin was laying the eggs.
That clinic at the surgeon was removing the cyst.
That coffee at the diner *was pouring the waiter*.
That gardener on the lawn *was stinging the wasp*.
The wand was waving a magician over the box.
That medicine was bringing a nurse in a cup.
Those fleas were bothering *that yard in the dog*.
The tabloids were harassing *the limo in the actress*.
A camel was hauling *the desert to the supplies*.
The infant was spilling *some carpet onto the milk*.

Sentences Presented during Localizer Scan

Three students were accused of cheating on the exam.
Twenty hungry men sat down in the tiny diner.
The gray mouse quickly scurried underneath the dusty rug.
Fifteen properties were sold by the realtor last month.
The spring crops were destroyed during the surprise blizzard.
The fish were swimming frantically in the leaky tank.
Security cameras were filming the robbery.
My rude professor unfairly grades my research papers.
An old car broke down in the middle of the freeway.
The boxer was punching his opponent in the jaw.
It was the butler who shot the colonel in the study.
Five cups of flour are needed for this recipe.
An eager salesman is approaching the customer.
The championship game was postponed because of the rain.
Her nervous boyfriend took the ring out of his pocket.
For two hours the basketball star signed autographs.
It was midnight when the baby finally fell asleep.
A team of eight mules pulled the covered wagon through the mud.
Some tourists hire a guide to show them the city.
The lava poured down the mountainside towards the village.

Noun Lists Presented during Localizer Scan

pillow dragon tile clay milk ladder truck foil shell
crew lullaby bag memory rust pine train glass rooster
steel parade turkey jar island frame zebra ramp puppet
tea igloo plant kangaroo movie toll joke ruler ants
salad rope skirt bridge tone frown crayon elbow rocker
ham trumpet engine brain money envelope flame trail broom
cloud banana rib dog screwdriver purse tent heart coin
shrimp wheel trust fairy elephant collar screen port bagel
juice scissors horse sponge nap example swamp ring braces
blade lounge cramp watches apple riches grade pants rubber
squash night box airplane leg cradle essay valley rules
vinegar book magnet whistle melon dust scale glove stage
river lamps soldier herd lump pineapple glue storm rabbit
speech jungle oil cove oatmeal mirror siren wave note
scent microphone price light marker submarine ice branch head
wasp library raft comb scandal telephone age map stem
hill barricade bait peace violin steam couch rose coil
scrap pond berry curtain necklace garage kite hope case
clamp school wind store dryer cabbage tuxedo bumper
sandal number platform sky rash backpack bush love sentence

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